

A New Species of Tritoniid Nudibranch, the First Found Feeding on a Zoanthid Anthozoan, with a Preliminary Phylogeny of the Tritoniidae

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This paper describes the first tritoniid nudibranch known to feed on zoanthid anthozoans. *Tritonia papalotla* n. sp. differs from all known species of Tritoniidae in its uniform brownish color pattern, undulating mantle margins, retractile digitiform respiratory organs, prominent dorsal vessels, uniseriate radula, and possession of both a receptaculum seminis and a bursa copulatrix. Owing to the extreme divergence of this species from other members of the Tritoniidae, a preliminary phylogenetic analysis was undertaken to establish its phylogenetic position relative to other members of the Tritoniidae. Despite the lack of robustness of the phylogeny, it is evident that the majority of tritoniid genera currently recognized are not monophyletic and a major systematic revision of the family is needed. *Tritonia papalotla* is included in a polytomy containing eight other tritoniid taxa in four different genera. The majority of these taxa are species currently placed in *Tritonia*. For this reason, *T. papalotla* is tentatively described as a *Tritonia*, the oldest genus within the family, until a thorough revision of the family is undertaken. The majority of *Tritonia papalotla*'s unique morphological attributes is shown by the present analysis to represent autapomorphies. For this reason, it is not included in a new superspecific taxon.

RESUMEN

En este trabajo se describe el primer nudibranquio tritónido conocido que se alimenta de antozoos zoantarios. *Tritonia papalotla* n. sp. se diferencia de todas las demás especies de Tritoniidae por su patrón de color pardo (café) uniforme, la presencia de márgenes del manto ondulados, órganos respiratorios retractiles digitiformes, venas dorsales prominentes, radula uniseriada, y la posesión de un receptáculo seminal y una bolsa copulatrix. Debido a la divergencia extrema de esta especie con otros miembros de Tritoniidae, un análisis filogenético preliminar ha sido llevado a cabo para establecer su posición en relación a otros miembros de la familia. Pese a la falta de robustez en la filogenia, es evidente que la mayoría de los géneros de Tritoniidae que están actualmente reconocidos no son monofiléticos y una revisión más completa de la familia es necesaria. *Tritonia papalotla* está incluida en una politomía que contiene otros ocho taxones de tritónidos pertenecientes a cuatro géneros diferentes. La mayoría de estos taxones son especies actualmente incluidas en *Tritonia*. Por esta razón, *T. papalotla* es tentativamente descrita como un miembro de *Tritonia*, hasta que se lleve a cabo una revisión de la familia. La mayoría de las peculiaridades morfológicas de *Tritonia papalotla* son, de acuerdo con el presente análisis, autoapomorfías. Por esta razón esta especie no se ha incluido en un nuevo taxón supraespecífico.

Odhner (1963) reviewed the genera and subgenera belonging to the family Tritoniidae, and established a classification scheme that is still in use. He regarded as valid the genera *Tritonia*

Cuvier, 1798, *Duvaucelia* Leach in Risso, 1826, *Marionia* Vayssière, 1877, *Tritoniopsis* Eliot, 1905, *Tritoniella* Eliot, 1907, *Marioniopsis* Odhner, 1934, *Paratritonia* Baba, 1949, and *Tochuina* Odhner, 1963. Subsequently, Thompson and Brown (1984) synonymized *Duvaucelia* with *Tritonia*. Odhner (1963) characterized the Tritoniidae by having blunt keels on the dorsal surface, the anus in the middle of the right body side, presence or absence of stomach plates, jaws with smooth margins and the digestive gland in a single mass. Willan (1988) in describing a new species of *Marioniopsis* from Australia, also included *Marianina rosea* (Pruvot-Fol, 1930) in the Tritoniidae rather than the Marianinidae.

Species of Tritoniidae feed on alcyonarian soft corals or gorgonians (Thompson and Brown 1984; Gosliner 1987; Gosliner and Ghiselin 1987; Willan 1988; Smith and Gosliner 2005, 2006, 2007). The present paper describes an extraordinary new species of Tritoniidae collected in Baja California and mainland México, which feeds on the unidentified zoanthid *Epizoanthus* sp., and has remarkable anatomical differences with other members of this group.

The material examined is deposited at the Natural History Museum of Los Angeles County (LACM) and the Department of Invertebrate Zoology and Geology of the California Academy of Sciences, San Francisco (CASIZ).

SPECIES DESCRIPTION

Tritoniidae Lamarck, 1809

Tritonia papalotla Bertsch, Valdes, and Gosliner, sp. nov.

Figures 1–5.

Tritonia sp. 1. Hermosillo et al., 2006:100.

TYPE MATERIAL.—HOLOTYPE: South end of Isla Magdalena, 200 m inside Bahía Magdalena (24.541994°N; 112.057198°W), Baja California Sur, México, 3–7 m depth, 16 June 1984, 1 specimen, 10 mm preserved length, leg. H. Bertsch (CASIZ 174163). PARATYPES: Punta Pescador, Bahía de los Ángeles, Baja California Sur, México, 7.6 m depth, 18 July 1994, 3 specimens 4–6 mm preserved length, leg. H. Bertsch (CASIZ 121107). One specimen, 6 mm preserved, dissected, Punta la Gringa, Bahía de los Ángeles, Baja California Sur, México, 4.5 m depth, 22 July 1995, 1 specimen 8 mm preserved length (CASIZ 121108). Punta la Gringa (29°02.57'N; 113°32.3'W), Bahía de los Ángeles, Baja California Sur, México, 4.5 m depth, 28 June 1996, 1 specimen, 8 mm preserved length, dissected, leg. H. Bertsch, M. Miller and S. Millen (CASIZ 121106). S. end of Isla Magdalena, 200 and inside Bahía Magdalena (25.282291°N; 112.118085°W), Baja California Sur, México, 3–7 m depth, 16 June 1984, 4 specimens, 9–10 mm preserved length, with egg mass on *Epizoanthus* sp., leg. H. Bertsch (CASIZ 174163), Punta la Gringa, Bahía de los Ángeles, Baja California, México, 3–4.5 m depth, 1 October 1984, 2 specimens 7 mm preserved length, leg. H. Bertsch and T. Gosliner (CASIZ 072927), rocky islets at se end of Isla Coronado, Bahía de los Ángeles, Baja California, México, 7–10 m depth, 4 October 1984, 2 specimens, 4–5 mm preserved length, leg. T. Gosliner (CASIZ 073506), Punta la Gringa, Bahía de los Ángeles, Baja California, México, 7 m depth, 29 June 1987, 3 specimens 7 mm preserved length, leg. H. Bertsch and T. Gosliner (CASIZ 071652), Punta la Gringa, Bahía de los Ángeles, Baja California, México, 3–4.5 m depth, 3 October 1984, 1 specimen 6 mm preserved length, leg. H. Bertsch (CASIZ 072929), Punta la Gringa, Bahía de los Ángeles, Baja California, México, 24 October 1986, 1 specimen, 6 mm preserved length, leg. H. Bertsch (LACM 2452). Punta la Gringa, Bahía de los Ángeles, Baja California, México, 4.5 m depth, 8 March 1986, 2 specimens 7 mm preserved length, leg. H. Bertsch and T. Smith (LACM 2453). Bajo de La Viuda (20°43.973'N; 105°23.967'W), Bahía de Banderas, Jalisco-Nayarit, México, 13 June 2003, 2 specimens 6–8 mm preserved length, leg. A. Hermosillo (LACM 2454).

DISTRIBUTION.—*Tritonia papalotla* has been reported from various locations within Bahía de los Ángeles (Punta la Gringa and Cuevitas, and the insular or outer peninsular sites of Islas Coro-

nadito and Mitlan, the reef between Islas Ventana and Cabeza de Caballo, and at Punta Pescador), B.C., on the inner side of the southern point of Isla Magdalena on the Pacific side of the Baja California Peninsula, and at the disjunct locality of Bahía de Banderas (at Bajo de la Viuda and Paraíso Escondido), Nayarit, over 1300 km south.

ETYMOLOGY.— The species name is based upon the Nahuatl word *papalotl*, which means butterfly (with the suffix *-a* added to agree adjectively with the feminine gender of the genus *Tritonia*). Nudibranchs are often popularly called butterflies of the sea (*mariposas de mar*).

In Aztec mythology, the butterfly is the symbol of the sun's movements, and was used to represent *Nahui Ollin*, the Fifth Sun, or present Age of the Earth, predicted to be destroyed by an earthquake. The two butterflies in the headdress of *Xochiquetzal* show her relationship with the sun god. *Xochiquetzal* was the goddess of flowers and love. According to the Aztec beliefs, she is the creator of the first humans and an intermediary with the gods. She is also credited with the first act of sex and the first childbirth. She lives in the mythical *Tamoachan* (place of our origin), guarding the sacred flowering bush *Xochitlicacan*. It is said that lovers need only to touch these flowers to gain happiness and fidelity (Fernández 1992:76, 97, 173; paraphrased translations from the Spanish by HB).

EXTERNAL MORPHOLOGY.— The length of the living animals reaches to 13 mm. Body elongate, with a deeply undulate mantle margin, forming 3–4 lateral lobes (Figs. 1A–B, 2A). The edge of the mantle margin has a series of irregular, gland-like lateral protuberances (Figs. 2A, 2C). Along the edge of the mantle is a series of digitiform, retractile respiratory structures. The cardiac area is elevated over the rest of the dorsum and is covered with several irregular tubercles. There are several ridges leading from the cardiac area in a radiating fashion (Fig. 2A). The main ridge runs towards the posterior end of the body, dividing the dorsum into two symmetric halves, and it is covered with irregular tubercles. There are some additional ridges leading from the main ridge. Secondary ridges are smooth and lower than the main ridge. There are about 8–9 secondary ridges on each side of the dorsum. The velum has two broad, conical oral tentacles (Fig. 3F). The front of the velum has 9–10 small, irregular, gland-like protuberances (instead of papillae), similar to those on the mantle margin. The rhinophoral sheaths are elevated, having several rounded tubercles on the edge and smaller tubercles on the lateral surface (Fig. 2B). Rhinophores with 4–5 vertical lamellae on each side and a posterior rounded knob. The lamellae are arranged vertically and are ramified. The rhinophores are densely covered with cilia (Fig. 2B). The reproductive opening is situated on the right side of the body, immediately behind the posterior end of the first lateral lobe of the mantle. The anal and renal apertures are also situated on the right side of the body, between the second and third lateral lobes of the mantle, and behind the pericardium.

The background color of the body is dark brown. The entire dorsum is covered with a number of rounded, opaque white spots, which are larger in the depressed areas surrounded by the dorsal ridges.

INTERNAL ANATOMY.— *Digestive system:* The oral tube is elongate and has a pair of strong retractor muscles attached medially and another pair attached posteriorly (Fig. 3B). The oval, muscular buccal bulb has two additional muscles. All muscles are attached to the body wall at the other end. Two long salivary glands connect with the buccal bulb at each side of the esophageal junction (Fig. 3D). The esophagus is initially thin. It emerges from the posterior end of the buccal bulb and runs towards the anterior region of the body. Right after passing through the central nervous system ring, it curves towards the posterior side of the body. Posteriorly, it expands into a wider tube that connects to the stomach (Fig. 3D). The stomach is oval and completely embedded into the digestive gland (Fig. 3A). At its posterior end, the stomach connects to three structures: two large and thin-walled sacs that open on the right side of the body, one anteriorly and one posteriorly; and

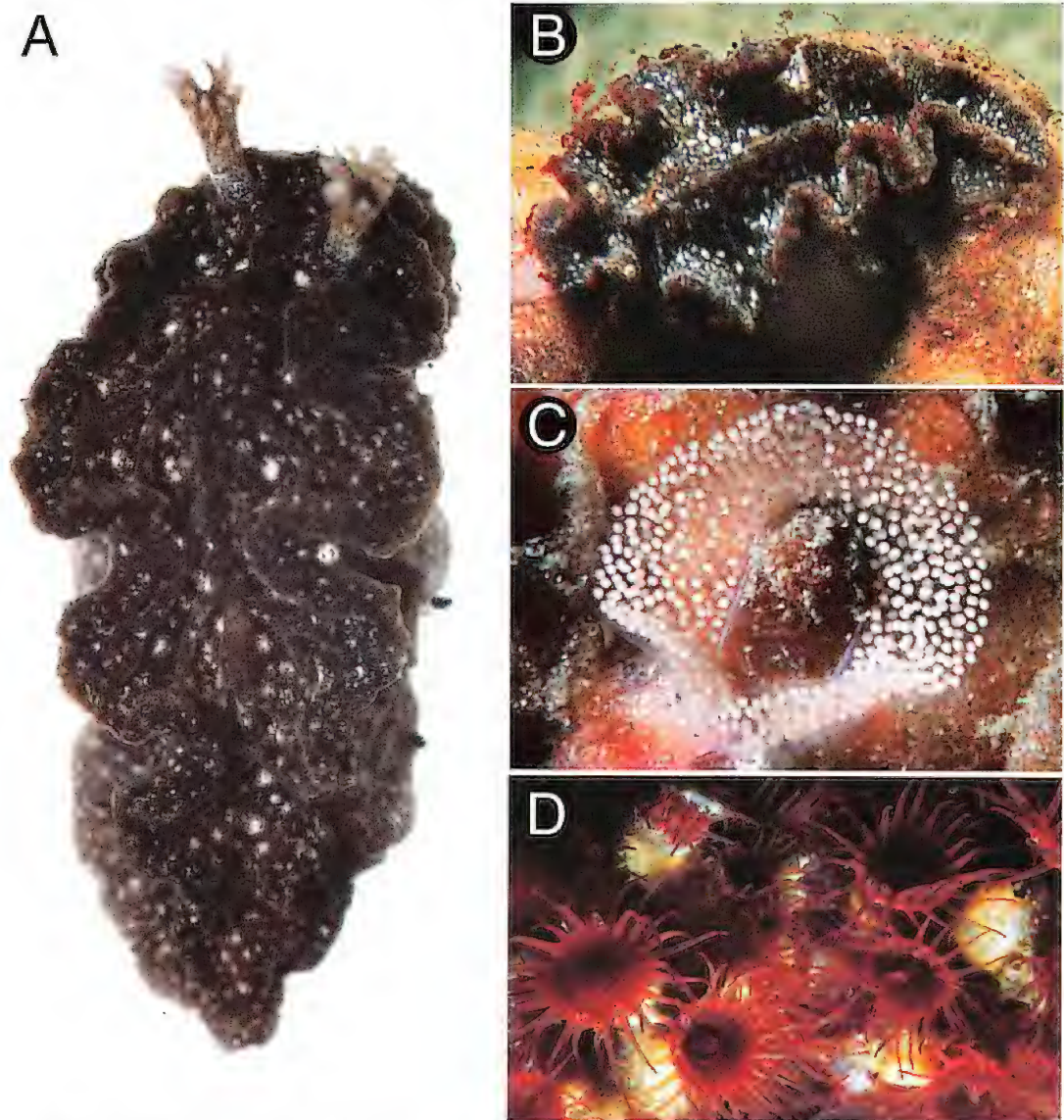


FIGURE 1. *Tritonia papalotla* n. sp. A. Living animal, Bahía de los Angeles, Baja California. B. Living animal on host prey, showing crimson secretions from mantle glands. C. Egg mass. D. *Epizoanthus* sp., all photos by. H. Bertsch.

the intestine (Fig. 3C). At the beginning, the intestine has a muscular, wide area with several thick, dark strips (Figs 3A, 3C). The intestine runs towards the anterior part of the body, curving to the right side before reaching the central nervous system; then it runs backwards and opens on the right medial region of the body (Fig. 3A).

The jaws consist of two elongate smooth plates with an elongate smooth masticatory border on each one (Fig. 4A). The radular formula is $24 \times (0.1.0)$ in a 7 mm long specimen (LACM 2453). The pectinate rachidian teeth are wide, with a series of long and sharp denticles (Fig. 4B–C). The 3–4 outermost denticles are simple and separated from each other. The following 5–7 denticles are fused together at their bases. There is no distinctive central cusp but it appears slightly longer than the surrounding denticles. All denticles are relatively equal in length. Lateral teeth are absent.

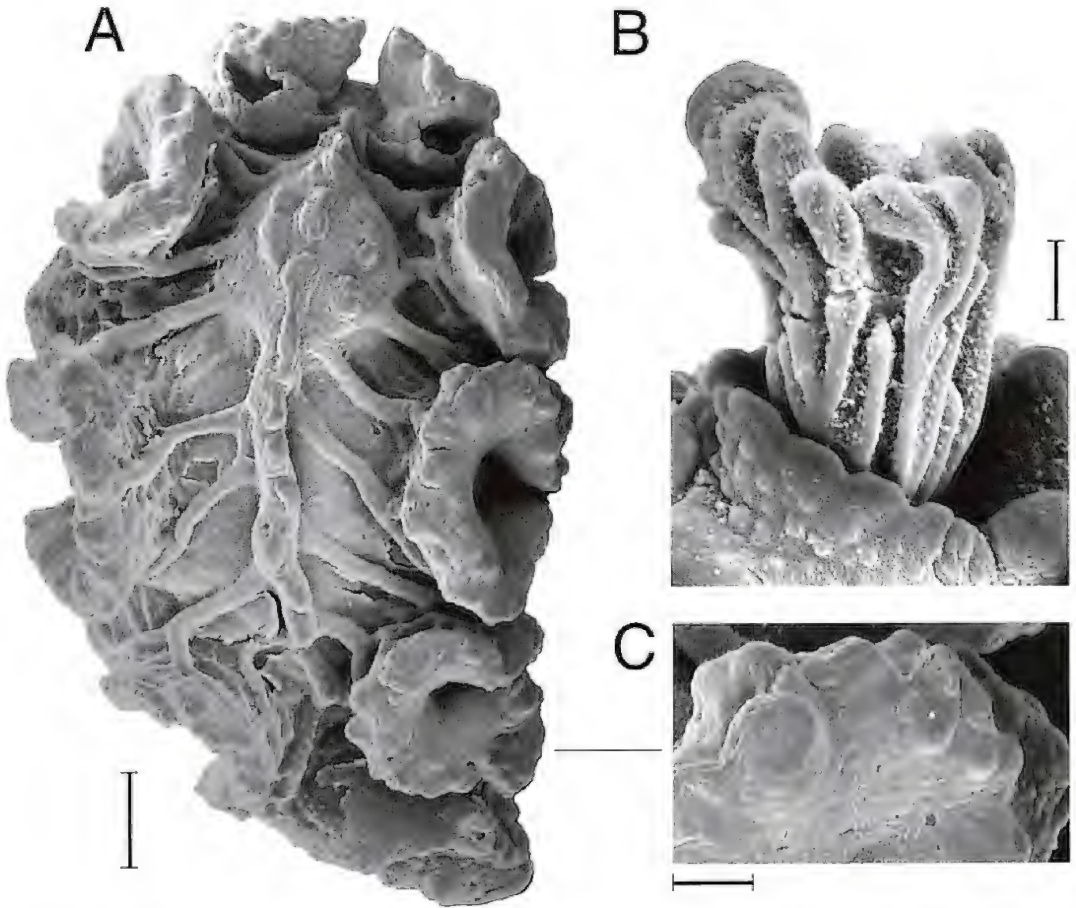


FIGURE 2. *Tritonia papalotla* n. sp. A. Dorsal surface of preserved animal, scale = 3 mm. B. Rhinophore, scale = 500 μ m. C. Mantle margin, scale = 500 μ m.

Reproductive system: The ampulla is oval and small, with the hermaphrodite duct and the gonoduct opening next to each other (Fig. 3E). The gonoduct is very long and branches into a short oviduct and the prostate. The prostate is tubular, flattened, folded and granular. It connects with a muscular duct that narrows and expands again into the long and strongly muscular ejaculatory portion of the deferent duct. The deferent duct opens into a common atrium with the vagina. The vagina is long and straight. Near its proximal end it joins the bursa copulatrix and the seminal receptacle (receptaculum seminis). The bursa copulatrix is rounded in shape, about twice as large as the seminal receptacle (Fig. 3E).

Central nervous system: The cerebral and pleural ganglia are fused together and distinct from the pedal ganglia (Fig. 5A). There are two cerebral nerves leading from each cerebral ganglion and three pleural nerves leading from each pleural ganglion. The buccal ganglia are near the rest of the central nervous system, joined to the cerebral ganglia by two relatively short nerves. There are no gastro-esophageal, rhinophoral or optical ganglia. The pedal ganglia are clearly separated, having three nerves leading from the right one and two nerves from the left one. The pedal and parapedal commissures are enveloped together. The visceral loop is very long, and the abdominal ganglion has not been observed.

Circulatory and excretory systems: The circulatory system consists of a small heart situated on

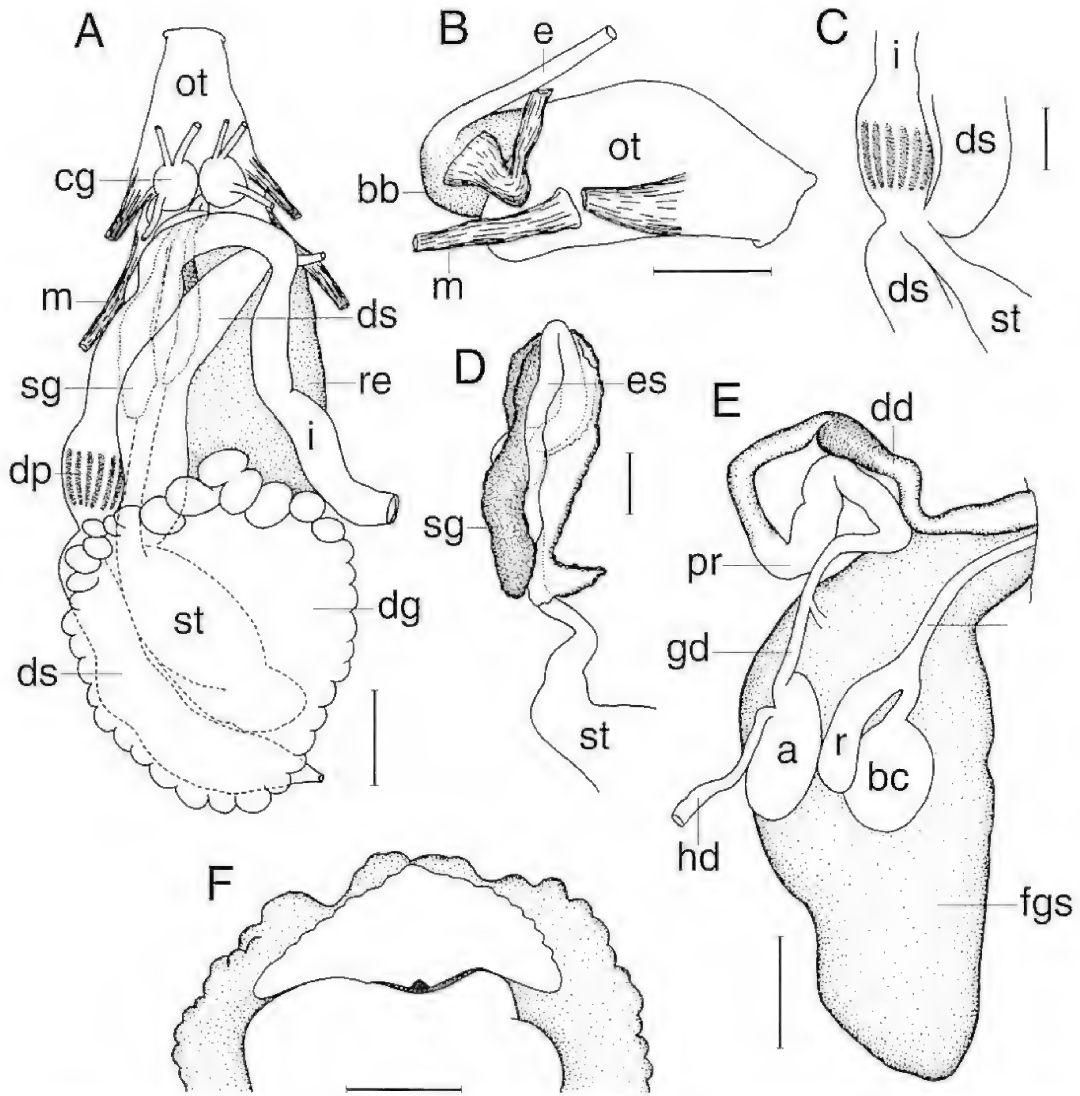


FIGURE 3. *Tritonia papalotla* n. sp. A. Arrangement of internal organs, cg = cerebralpleural ganglia, dg = digestive gland, dp = digestive plate ridges, ds = digestive sac, i = intestine, m = retractor muscles of oral tube, ot = oral tube, re = reproductive system, sg = salivary glands, st = stomach, scale = 1 mm. B. Lateral view of oral tube, bb = buccal bulb, e = esophagus, ot = oral tube, scale = 1 mm. C. Branching of digestive gland ducts showing muscular ridges, i = intestine, ds = digestive sacs, st = stomach, scale = 500 μ m. D. Anterior portion of digestive tract, es = esophagus, sg = salivary gland, st = stomach, scale = 500 μ m. E. Reproductive system, a = ampulla, bc = bursa copulatrix, dd = deferent duct, fgs = female glands, gd = gonoduct, hd = preampullary hermaphroditic duct, pr = prostate, r = receptaculum seminis, scale = 1 mm. F. Ventral side of body showing foot and oral veil, scale = 1 mm.

the anterior right side of the body (Fig. 5B). The heart is isolated from the rest of the viscera by a wall of tissue. The heart opens into the pericardium on its left side. The excretory system has a large, ramified kidney (Fig. 5B).

BIOLOGY

LIFE CYCLE AND POPULATION DYNAMICS.—Bahía de los Ángeles has been the site of over

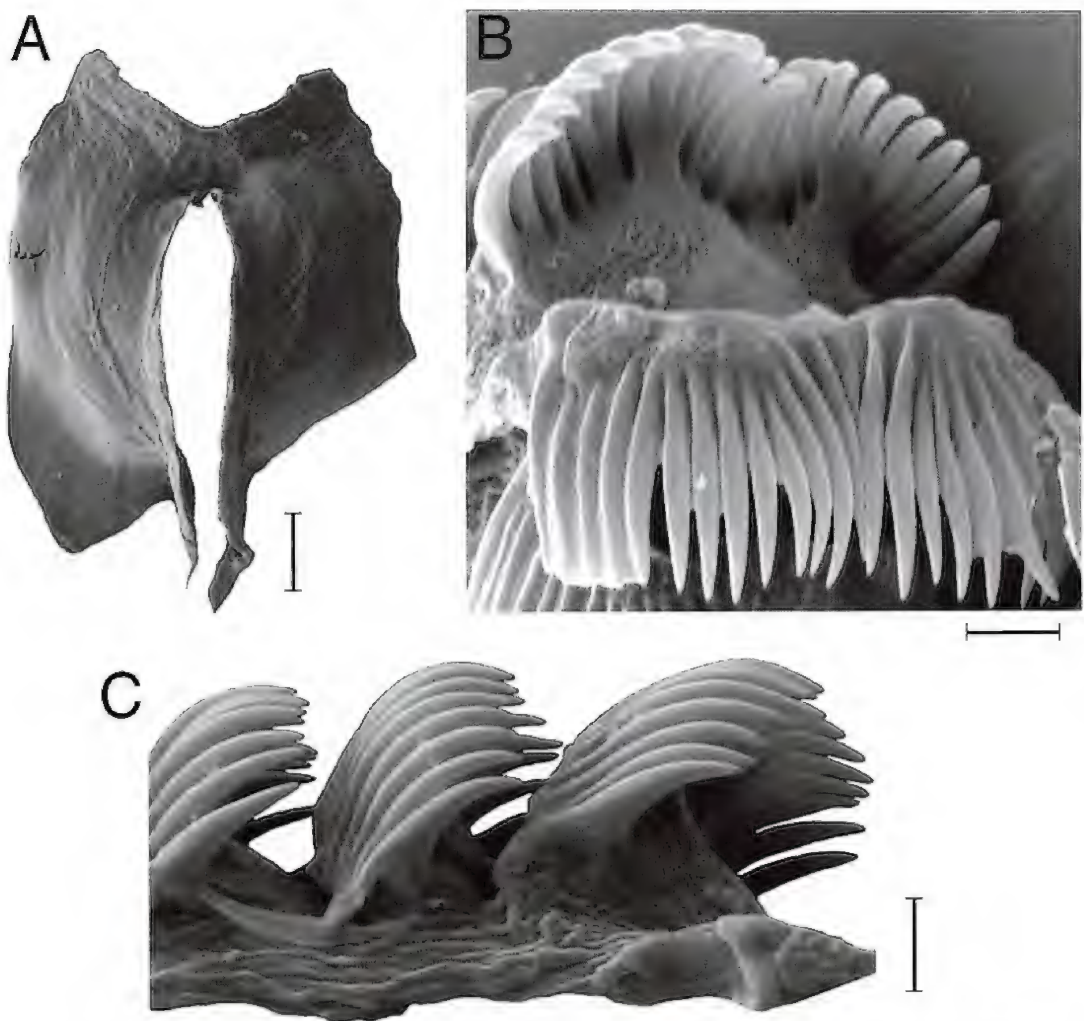


FIGURE 4. *Tritonia papalotla* n. sp. scanning electron micrographs. A. Jaws, scale = 200 μm . B. Rachidian teeth, scale = 10 μm . C. Lateral view of rachidian teeth, scale = 10 μm .

three decades of ongoing subtidal ecological research on opisthobranchs by the senior author. These studies have resulted in an understanding of opisthobranch natural history at population and community levels; they have also been used in contrasting feeding biogeography.

Overall abundance of nine opisthobranch populations declined during the 10-year period of 1992–2001 (Bertsch 2008), due to the significant decrease in numbers of the sacoglossan *Elysia diomedea* Bergh, 1894, and the nudibranch *Phestilla lugubris* (Bergh, 1870). However, the seven other most common opisthobranch species showed no significant change in population densities. Analysis of data (Table 1) from the 21-year period of 1982–2003, demonstrates that the annual density/hour of search for *T. papalotla* decreased significantly (Fig. 6), with a slope correlation of -0.11042 , $P = > 0.001$. Hermosillo (2006) found a similar decline in Bahía de Banderas between 2002–January 2005.

During the 3-year period January 2002–January 2005, the 25 most common species of opisthobranchs varied seasonally in abundance (Bertsch, pers. observ.), overall exhibiting an inverse cor-

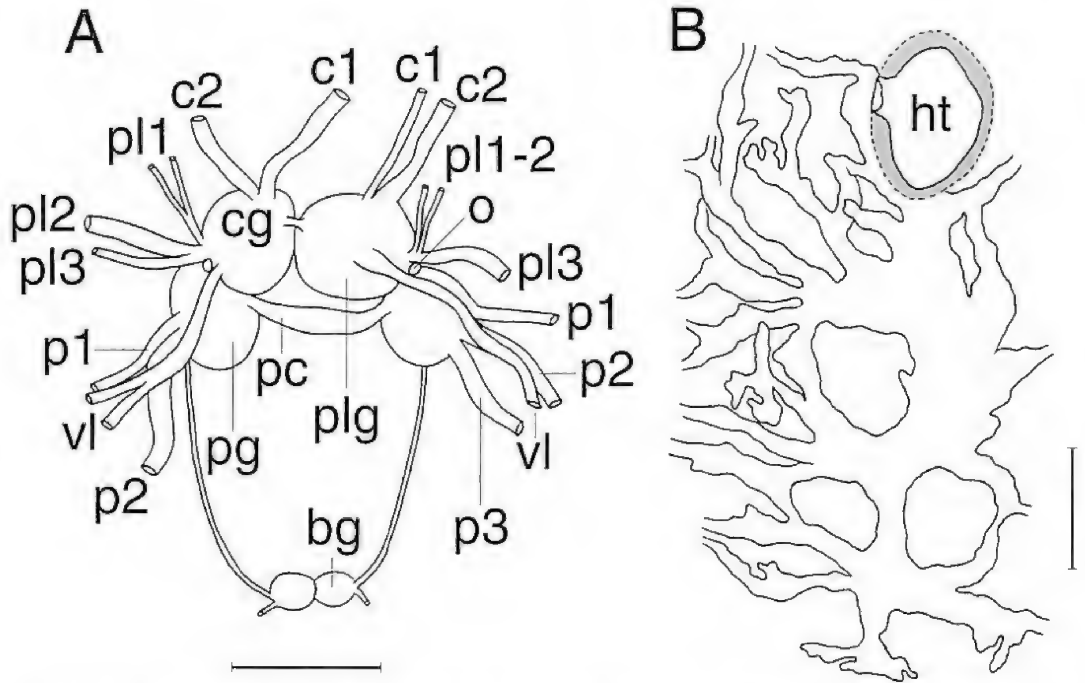


FIGURE 5. *Tritonia papalotla* n. sp. A. Central nervous system, bg = buccal ganglion, c1 = cerebral nerve 1, c2 = cerebral nerve 2, cg = cerebral ganglion, o = otocyst, p1 = pedal nerve 1, p2 = pedal nerve 2, p3 = pedal nerve 3, pc = pedal commissure, pg = pedal ganglion, plg = pleural ganglion, pl1 = pleural nerve 1, pl2 = pleural nerve 2, pl3 = pleural nerve 3, vl = visceral loop, scale = 500 μ m. B. Dissection of the kidney and heart, ht = heart, scale = 1 mm.

relation between temperature and density (Fig. 7A, Table 2). Those less abundant species showing a positive correlation, with highest abundances in the warm-water summer months, included *Phidiana lascrucensis* Bertsch and Ferreira, 1974, *Discodoris ketos* (Marcus and Marcus, 1967), and *Tyrinna evelinae* (Marcus, 1958). Over the 10-year period of 1992–2001, *Chromodoris norrisi* Farmer, 1963, showed such a warmer-water distribution (Bertsch 2008). In contrast, the presence (measured as density/hour of search) of *Tritonia papalotla* seems to have no relation at all with temperature, exhibiting high abundances in the warm- and cold-water months of May, June, September and December (Fig. 7B, Table 3). In Bahía de Banderas (Hermosillo 2006), *Tritonia papalotla* was most abundant during June and July (Fig. 7C, Table 4).

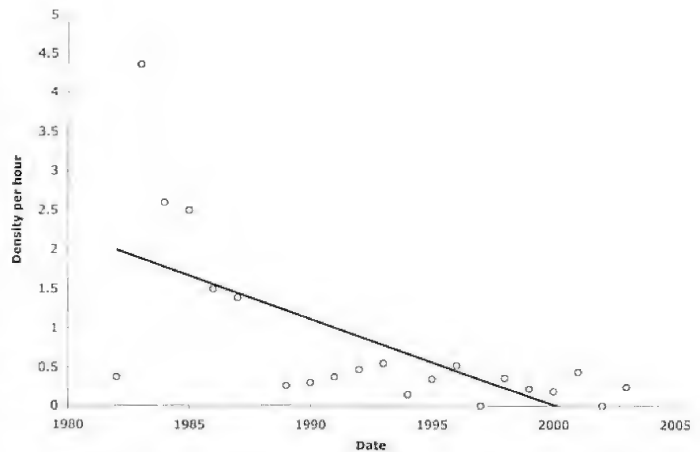


FIGURE 6. Graph showing annual decline in the density of *Tritonia papalotla* n. sp. at Bahía de los Ángeles, 1982–2005.

Doriopsilla gemela Gosliner, Schaefer and Millen, 1999, exhibits a distinct annual cycle with quite different average monthly sizes; 20–35 mm adults occur April–June, whereas < 10 mm juveniles abound September–November (Bertsch 2002). Such annual cycles have also been observed (Bertsch, pers. obser.) in *Doriopsilla albopunctata* (Cooper, 1863), *Dendrodoris fumata* Rüppell and Leuckart, 1831, and the pleurobranchoid *Berthellina ilisima* (Marcus and Marcus, 1967). Sizes of *T. papalotla* individuals varied monthly (Table 5), from a minimum mean of 5.65 mm (December) to maximum means of 9.6 and 9.4 mm (in May and July), but without the distinct annual cycle of *Doriopsilla gemela*.

Distinct differences occur in community structure (Bertsch, Miller and Grant 1998) and percentages of feeding preferences among species (Bertsch and Hermosillo 2007) between the inner bay shoreline at Punta la Gringa and Cuevitas, and the bay's islands and outer southern Gulf coast. The prevalent occurrence of *T. papalotla* at Punta la Gringa and Cuevitas (132 out of 153 animals, 86%) reflects these differences of species composition.

EGG MASS.—The egg mass consists of a one-whorl ribbon with a number of opaque white eggs. They have been observed at the BLA inner shore sites from May through December, with maximum numbers found in June, July, September and November. (Table 6). A single egg is contained within a capsule. Capsules are approximately 270 μm in diameter and eggs are about 240 μm in diameter, indicating that *Tritonia papalotla* likely has lecithotrophic or direct development. This is in stark contrast to the vast majority of eastern Pacific

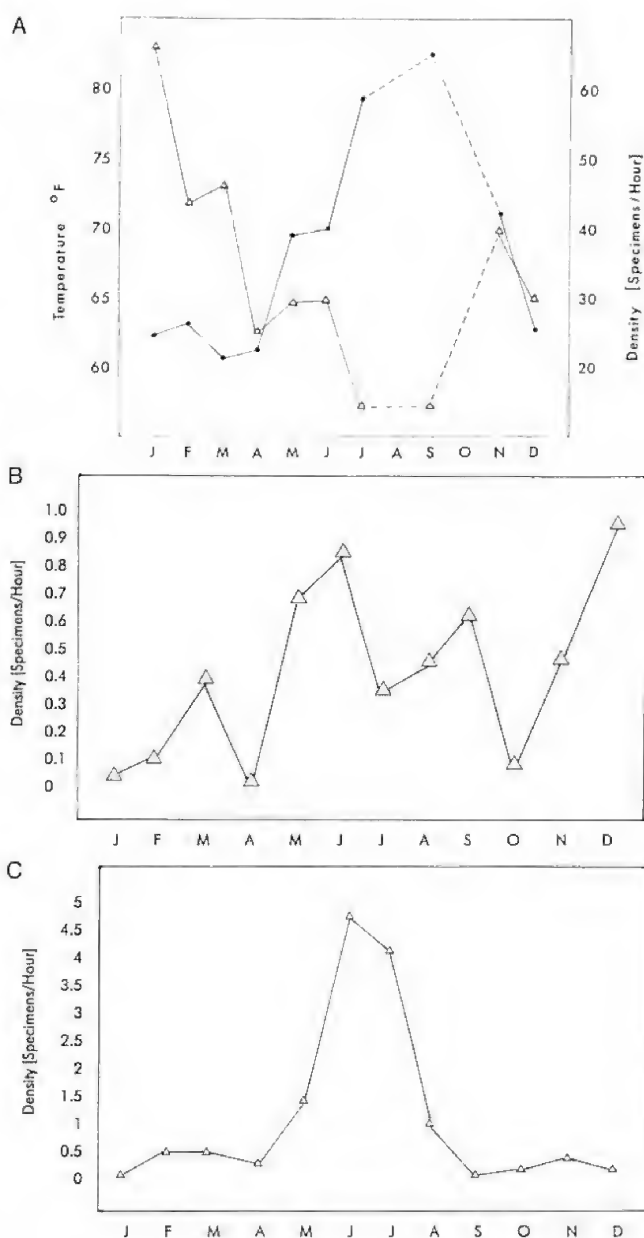


FIGURE 7. A. Graph showing seasonal inverse relationship between temperature and density of the 25 most common opisthobranch species at Bahía de los Ángeles. B. Variation in monthly density of *Tritonia papalotla* n. sp. at Bahía de los Ángeles, 1982-2003. C. Seasonal variation in monthly density of *Tritonia papalotla* n. sp. at Bahía de Banderas (Nayarit), 2002- January 2005.

species, which are known to be largely planktotrophic in development (Goddard and Hermosillo 2008)

NATURAL HISTORY AND BEHAVIOR.—*Tritonia papalotla* has been found only on its prey item, an unnamed species of *Epizoanthus* (Cnidaria: Anthozoa: Zoantharia). The nudibranch has been most frequently found on anemones attached to upright gorgonians (e.g., *Muricea*, *Eugorgia*, and *Psammogorgia*), but sometimes on anemone colonies forming encrusting sheets on the side of a rock surface or a rock overhang. Often living between the polyps of this zoanthid are many individuals of the architectonicid prosobranch gastropod *Heliacus mazatlanicus* Pilsbry and Lowe, 1932.

The glands of the mantle margin produce a crimson dense secretion when the animal is annoyed (Fig. 1B).

REMARKS

This species is clearly distinct from other tritoniids known from the eastern Pacific, *Tritonia festiva* (Stearns, 1873), *T. diomedea* Bergh, 1894, *T. pickensi* Marcus and Marcus, 1967, *T. myrakeenae* Bertsch and Mozqueira, 1986, and *Tochuina tetraquetra* (Pallas, 1788). All of these taxa are white, pink or orange in body

color rather than the brown and white color of *T. papalotla*. None of these species have the prominent dorsal vessels found in *T. papalotla* and have prominently displayed branched secondary gills, rather than the digitiform retractile ones of *T. papalotla*. Internally, none of these species have a pectinate rachidian tooth as in *T. papalotla* and all have numerous lateral teeth, which are entirely absent in *T. papalotla*.

Tritonia papalotla can be distinguished immediately from all other Tritoniidae by the presence

TABLE 1. Annual density (per hour of search) of *Tritonia papalotla* at Punta la Gringa and Cuevitas, Bahía de los Ángeles, 1982–2003 (data for graph, Figure 6).

Year	Search hours	Specimens	Density/Hour
1982	5.34	2	0.375
1983	3.9	17	4.36
1984	8.08	21	2.6
1985	4.0	10	2.5
1986	4.0	6	1.5
1987	3.61	5	1.39
1988	—	—	—
1989	7.62	2	0.262
1990	16.39	5	0.305
1991	15.91	6	0.377
1992	27.5	13	0.473
1993	23.57	13	0.552
1994	42.08	6	0.143
1995	31.67	11	0.347
1996	24.82	13	0.524
1997	36.54	0	0
1998	13.71	5	0.365
1999	18.31	4	0.218
2000	16.31	3	0.186
2001	18.05	8	0.443
2002	7.22	0	0
2003	12.33	3	0.243

TABLE 2. Monthly density/hour of 25 most common opisthobranchs at inshore sites of Bahía de los Ángeles, January 1992–January 1995 (data for graph, Fig. 7A).

Month	Search hours	Specimens	Density/Hour
January	7.69	507	65.9
February	5.18	226	43.6
March	6.53	302	46.2
April	7.84	193	24.6
May	3.68	108	29.3
June	10.82	327	30.2
July	19.65	285	14.5
August	—	—	—
September	7.35	107	14.6
October	—	—	—
November	15.37	618	40.2
December	12.86	386	30.0

of a series of unique, derived features. It is the only tritoniid with a series of vessels radiating from the cardiac region. This feature is somewhat reminiscent of that found in the sacoglossan Plakobranchidae (Gosliner 1995). Additionally, the presence of secondary gills that are completely retractile into pits along the notal margin is unique to this species. Internally, this species has the unique attribute of having a radula with rachidian teeth that are pectinate rather than being tricuspid. This form of radula is convergent with aeolid species within the Acolidiidae, which feed on sea anemones and zoanthids. Also, the radula completely lacks lateral teeth. Most tritoniids have numerous lateral teeth on either side of the rachidian tooth. Only *Marianina rosea* has a reduced number of lateral teeth, with 4–6 laterals flanking either side of the multidenticulate rachidian. The posterior end of the stomach of *T. papalotla*, is muscularized and has a series of ridges that may be vestiges of stomach plates as has been found in *Tritonia bollandi* Smith and Gosliner, 2005. The reproductive system of *T. papalotla* is also unique in having a bursa

copulatrix and a receptaculum seminis. The arrangement of the reproductive system is similar to that described for species of *Berthella* such as *B. canariensis* (Cervera et al., 2000). Both *Marianina elongoviridis* Smith and Gosliner, 2007, and *M. elongoreticulata* Smith and Gosliner, 2007 have a single bursa but the distal end is much narrower than the main portion of the sac. Given that *T. papalotla* has so many unique attributes, it is tempting to place it in a new higher taxon. However, contemporary phylogenetic theory requires that relationships must be determined on the basis of shared, derived features rather than unique ones. For that reason, we found it necessary to include a preliminary morphological phylogenetic analysis of Tritoniidae to determine where *T. papalotla* is likely placed relative to other tritoniid taxa. Based upon this analysis further discus-

TABLE 3. Monthly density/hour of *Tritonia papalotla* at inshore sites of BLA, 1982–2003 (data for graph, Figure 7B).

Month	Search hours	Specimens	Density/Hour
January	20.83	1	0.048
February	26.3	3	0.114
March	20.19	8	0.396
April	26.13	1	0.038
May	20.22	14	0.692
June	39.15	34	0.868
July	49.14	18	0.366
August	15.12	7	0.463
September	32.22	20	0.621
October	18.22	2	0.11
November	43.94	22	0.501
December	24.14	23	0.953
<i>Seasonal Summary:</i>			
January–May	113.77	27	0.237
June–December	221.91	126	0.568

TABLE 4. Monthly density/hour of *Tritonia papalotla* at Bahía de Banderas, Nayarit, 2002–January 2005; data courtesy of Alicia Hermsillo (data for graph, Figure 7C).

Month	Search hours	Specimens	Density/Hour
January	11.37	0	0
February	4.6	2	0.43
March	7.4	3	0.41
April	6.2	2	0.32
May	7.3	10	1.37
June	10.85	51	4.7
July	8.1	32	3.95
August	9.47	11	1.16
September	7.03	0	0
October	7.55	1	0.13
November	10.6	3	0.28
December	6.9	1	0.14
<i>Seasonal Summary:</i>			
January–May	36.87	17	0.46
June–December	60.5	99	1.64

sion of the systematic placement of *T. papalotla* will follow.

PHYLOGENETIC RELATIONSHIPS

The phylogenetic relationships of the family Tritoniidae are poorly understood. Schmekel (1985) based on a hand-made phylogenetic reconstruction found the Tritoniidae to be monophyletic group, being the sister to the Lomanotidae. The major synapomorphy for this clade would be the presence of palmate rhinophoral clavi. On the contrary, Wägele and Willan (2000) in their phylogenetic hypothesis of the Nudibranchia showed that the the Dendronotacea is the sister to the Tritoniidae, and Lomanotidae the sister to this other clade. The detailed phylogenetic relationships within members of the Tritoniidae remain unknown. Generic distinctions have traditionally been based on presence or absence of stomach plates, shape of the rachidian tooth and shape of the velar appendages (Odhner 1936, 1963).

In order to test these hypotheses, a preliminary morphological phylogenetic analysis was undertaken. This analysis included 22 species of Tritoniidae and *Berthella canariensis* Cervera, Gosliner, García Gómez and Ortea, 2000, was used as the outgroup. Two additional ingroup taxa, *Melibe rosea* Rang, 1829, and *Notobryon wardi* Odhner, 1936, were included to test the monophyly of Tritoniidae. Thirty characters were scored for 25 taxa (Table 7).

Analysis

In order to calculate the most parsimonious phylogenetic tree, data were analyzed by means of Phylogenetic Analysis Using Parsimony (PAUP) version 4.0b4a (Swofford 2002) using the branch and bound algorithm via stepwise addition. Both the Accelerated Transformation (ACCTRAN) and Delayed Transformation (DELTRAN) optimizations were used for character transformation. In both cases the multistate characters were treated as unordered. See Kitching et al. (1998) for a thorough explanation of these methods and their advantages. A decay analysis (Bremer 1994) was carried out to estimate branch support. Synapomorphies were obtained using the character trace option in MacClade 4.08a (Maddison and Maddison 2005) using the trees from the PAUP analysis.

PHYLOGENETIC RESULTS AND DISCUSSION

The present phylogenetic analysis of 1000 replicates produced 15 most parsimonious trees with a length of 83 steps. The consistency index is 0.518 with a retention index of 0.669. Synapomorphies were mapped using the character trace option in MacClade 4.08 (Maddison and Maddison 2005) employing the majority rule tree from the PAUP analysis. Bremer analyses were performed on the strict consensus tree to estimate branch support (Bremer 1994).The overall support based on a Bremer decay analysis is relatively low, with values of only 1 for all nodes. In the result-

TABLE 5. Monthly average sizes of *Tritonia papalotla* (from available data) at Bahía de los Ángeles, 1982–2008.

Month	Specimens	Mean (mm)	Standard deviation
January	N/A		
February	N/A		
March	8	8.0	2
April	N/A		
May	13	9.615	2.567
June	41	8.27	2.0497
July	22	9.39	2.278
August	N/A		
September	13	7.23	2.89
October	3	9.0	3.606
November	24	8.67	3.5
December	17	5.65	1.84

TABLE 6. Egg masses of *Tritonia papalotla* counted at Bahía de los Ángeles, 1982–2008.

Month	Number
January	0
February	0
March	0
April	0
May	5
June	27
July	27
August	4
September	21
October	11
November	27
December	8

TABLE 7. Thirty characters and character states were scored for 25 taxa.

1. Velum	17. Stomach plate number
0 = not expanded	0 = up to 40
1 = expanded into oral veil or hood	1 = 40-90
2. Velum shape	2 = 100 or more
0 = bilobed	? = not applicable
1 = undivided	18. Radula
? = not applicable	0 = present
3. Velar papillae	1 = absent, autapomorphic for <i>Melibe rosea</i>
0 = absent	19. Rachidian tooth
1 = present	0 = absent
4. Velum papillae	1 = present
0 = few (8 or less)	20. Rachidian tooth central denticle
1 = numerous single row	0 = present
2 = numerous more than one row	1 = absent
? = not applicable	? = not applicable
5. Velum papillae shape	21. Rachidian tooth shape
0 = compound	0 = unicuspid
1 = simple	1 = tricuspid
? = not applicable	2 = unicuspid with several small denticles
6. Rhinophore form	3 = pectinate
0 = rolled	4 = other <i>Tritoniella belli</i>
1 = solid	? = not applicable
7. Rhinophoral lamellae	22. Inner lateral tooth
0 = horizontal	0 = differentiated
1 = vertical	1 = undifferentiated
? = not applicable	2 = absent
8. Rhinophoral sheath	23. Inner lateral accessory denticle
0 = simple	0 = absent
1 = ornamented	1 = present
9. Notal texture	? = not applicable
0 = tubercular	24. Radular width
1 = smooth	0 = wide
10. Dorsal processes	1 = narrow
0 = absent	? = not applicable
1 = present	25. Prostate
11. Gill	0 = indistinct
0 = present	1 = distinct
1 = absent	26. Receptaculum seminis
12. Dendritic gills	0 = present
0 = present	1 = absent
1 = absent	27. Bursa copulatrix
13. Dendritic gill number	0 = elongate
0 = 1-8	1 = pyriform
1 = 12-30	2 = with distal lobe
2 = more than 30	3 = spherical
? = not applicable	28. Penis shape
14. Jaw masticatory border	0 = flagelliform
0 = more than 7 rows of denticles	1 = conical or rounded
1 = 2-7 rows	2 = paddle shape
2 = 1 row	3 = apical ring
3 = smooth	29. Digestive gland
15. Crop	0 = compact mass
0 = absent	1 = diffuse
1 = present	30. Optic nerve
16. Stomach plates	0 = elongate
0 = present	1 = sessile
1 = absent	
2 = thin cuticular girdle	

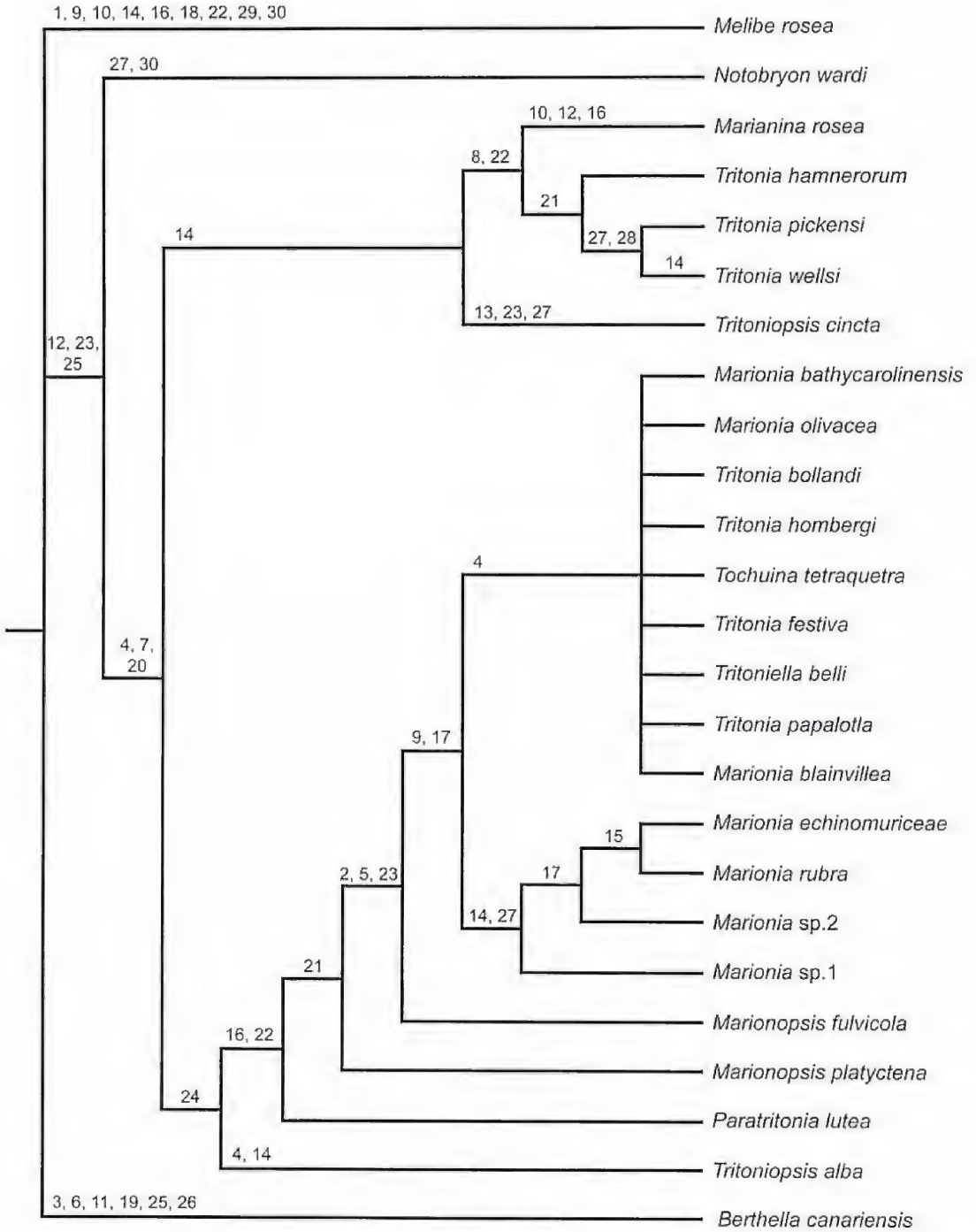


FIGURE 8. Strict consensus phylogeny of Tritoniidae, numbers at nodes refer to characters listed in Table 7.

ing phylogeny, Tritoniidae is monophyletic, but weakly supported with three synapomorphies (papillae number, rhinophoral lamellae and central denticle). These values indicate that the resulting tree lacks robustness. Future studies to produce a more robust tritoniid phylogeny might include additional ingroup taxa, additional morphological characters that vary within Tritoniidae and an evaluation of molecular phylogenetic variability within Tritoniidae.

Despite the lack of robustness of the tree, there are several preliminary results of note. First, the Tritoniidae appears to represent a monophyletic group. Most germane to the present study is the fact that *Tritonia papalotla* is nested with a clade of species of *Tritonia*, *Marionia* and the monotypic taxa, *Tochuina tetraquetra* and *Tritoniella belli*. This indicates that the present species, despite its many autapomorphies should be included with other species of Tritoniidae but that generic distinctions are at present poorly resolved. The preliminary tree is indicative that distinctions between tritoniid genera are at best problematic. None of the currently recognized higher taxa of Tritoniidae are monophyletic in the current analysis. A group of taxa that include *Tritoniopsis cincta*, *Marianina rosea* and three Caribbean and one tropical eastern Pacific species of *Tritonia* is the sister to the rest of the Tritoniidae. This clade is poorly supported by only a single apomorphy. The sister to this clade is comprised of *Tritoniopsis alba*, *Paratritonia lutea*, species of *Marionia*, *Tritoniella belli*, *Tochuina tetraquetra* and the remaining species of *Tritonia*. *Marionia* represents a grade of taxa and is paraphyletic when other taxa are considered as distinct. As *Tritonia papalotla* is a member of a poorly resolved clade containing taxa of the genera *Tritonia*, *Marionia*, *Tritoniella* and *Tochuina*, its generic placement is problematic. It is tentatively placed in *Tritonia*, as it lacks stomach plates, while species of *Marionia* and *Tochuina* have distinct chitinous plates and *Tritoniella belli* has a distinct cuticular lining to the stomach (Wägele 1989). Some species of *Tritonia*, such as *T. festiva* (Stearns, 1873), have a vestigial girdle of chitinous ridges as in *T. papalotla*. Clearly, a comprehensive revision of the Tritoniidae is needed to clarify phylogenetic relationships and determine boundaries of monophyletic higher taxa. However this is beyond the scope of the current descriptive nature of this paper.

ACKNOWLEDGMENTS

We thank Vic Smith for providing us with his preliminary data from his Master's thesis that were included in the present phylogenetic analysis. This research has been funded by the National Science Foundation PEET (DEB 0329054) Phylogeny of the Nudibranchia to T. Gosliner and A. Valdés. We thank our colleagues and friends in Bahía de los Ángeles (especially Carolina Espinoza, and Antonio and Bety Resendiz) for their support and help, and Tom Smith, Sandra Millen, Michael D. Miller, Brian Coleman, Alan Grant and Rosa del Carmen Campay for research assistance. Jeffrey Crooks (Research Coordinator at the Tijuana River National Estuarine Research Reserve, Imperial Beach) provided statistical analyses, and Alicia Hermosillo (CUCBA, Universidad de Guadalajara) shared her collecting data from Bahía de Banderas, Nayarit.

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